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Gammarid and Corophiid Amphipods (Crustacea, Peracarida, Amphipoda) of Laguna de Tamiahua, Veracruz and Laguna Madre, Tamaulipas, Mexico: Spatial and Temporal Distribution

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Gammarid and Corophiid Amphipods (Crustacea, Peracarida, Amphipoda) of Laguna de Tamiahua, Veracruz and Laguna Madre, Tamaulipas, Mexico: Spatial and Temporal Distribution

Andrea Raz-Guzmán and Ana Laura Villegas

Gammarid and corophiid amphipods were collected in Laguna de Tamiahua and Laguna Madre from seagrass beds, macroalgae, and bare substrates with a Renfro beam net and an otter trawl. Tamiahua provided 17 species, of which *Cymadusa compta* was the dominant species (66.3%), while Madre provided 24 species with *C. compta* (60.8%) and *Elasmopus levis* (20.2%) as the dominant species. Amphipod distribution was widespread in both lagoons, though concentrated along the inner margin of the sand barriers in *Halodule wrightii* beds. In Tamiahua, five species were present throughout the lagoon, *E. levis* in the north and center, *Ampelisca vadorum* in the north and south, and *Nototropis minikoi* and *Melita nitida* in the center and south, with *Ampithoe valida* only in the north, *Ampithoe longimana* only in the center, and *Apohyale prevostii* only in the south. In Madre, eight species were present throughout the lagoon, *Gammarus mucronatus* only in the north and south, *Ampelisca vadorum* only in the center and Catán, four species only in the north, two only in the center, and two only in the south. The number of species recorded in August and December in general did not vary, whereas the greater density values of August suggest optimum conditions for reproduction and survival, and the lower values of December may follow the harsher climatic conditions and/or predation by visiting migratory birds and fish that winter in these lagoons. Compared with Términos, Alvarado and each other, Tamiahua and Madre are the most similar, since they share 12 species, environmental characteristics, and seagrass distribution.

Amphipods constitute a highly diverse group of peracarid crustaceans with respect not only to the number of species described but also to their varied morphology and ecology. Most species are eurythermal, euryhaline, and benthic and are found in freshwater, estuarine, and marine environments, on all types of substrates, on submerged aquatic vegetation, and on other faunal species (Corona et al., 2000; Thomas and Klebba, 2007). Their distribution is cosmopolitan, and some reach depths of 600 m. They play an important part in the structure and function of estuarine communities through their high abundance (Nelson, 1979; Tanner, 2006), reproductive strategies (Johnson et al., 2000), behavior, and feeding habits (DeBlois and Leggett, 1993; Kamermans et al., 2002). They recycle nutrients, favor sediment bioturbation and stabilization, and may be parasites and disease vectors. They link foraging and detritivore food chains and are important prey of cephalopods (Pérez and Haimovici, 1995), fish, birds, and other crustaceans (Hill and Elmgren, 1992; Duffy and Hay, 2000). Their responsiveness to a variety of toxic and polluting agents makes them excellent bioindicators of environmental quality, for which reason they are used as biomonitors in biological models (Thomas, 1993b) and in biogeographic studies (Paz-Ríos and Ardisson, 2013).

Laguna de Tamiahua and Laguna Madre are important nursery and feeding areas for freshwater, estuarine, and marine species. Madre also provides feeding and resting areas for wintering migratory birds (Tunnell and Judd, 2002). Both lagoons sustain traditional fisheries of oysters, shrimp, swimming crabs, and mullets. The salinity gradient, the variety of substrates, and the submerged aquatic vegetation generate a notable heterogeneity of habitats that are available for resident and visiting species, an example of which is the high values of invertebrate abundance that have been recorded (Raz-Guzmán and Barba, 2000; Cid and Raz-Guzmán, 2011).

Studies on amphipods of the Mexican Gulf of Mexico coastal lagoons include those of Ledoyer (1986), Corona et al. (2000), and Cházaro et al. (2002) for Laguna de Términos in Campeche; Winfield et al. (1997, 2001, 2007) and Winfield and Ortiz (2011) for Laguna de Alvarado in Veracruz; Cházaro et al. (2002) and Winfield and Ortiz (2011) for Laguna Camaronera in Veracruz; Winfield and Ortiz (2011) for Laguna de

Sontecomapan and Laguna de Tamiahua in Veracruz; and Barba and Sánchez (2005) and Ortega (2013) for Laguna Madre in Tamaulipas. A detailed description of amphipod distribution in Laguna de Tamiahua and Laguna Madre has not been carried out, however. The present study was thus designed to record the spatial and temporal distribution of amphipods in both systems in summer and winter.

Methods

Study area.—Laguna de Tamiahua is the third largest coastal lagoon in the Mexican Gulf of Mexico with 88,000 ha. It is 90 km long and 22 km wide. It is located at 21°16′–22°05′N and 97°23′–97°43′W. It is bordered to the north by the Río Pánuco and to the south by the Río Tuxpam. It has two inlets, Tampachichi to the north of the lagoon and Corazones to the south, with the sandy barrier of Cabo Rojo to the east. Cabo Rojo is a zoogeographically significant area, since it marks the transition between the Carolinean–Temperate and the Caribbean–Tropical provinces for shallow-water marine communities (Thurman, 1987). Inside the lagoon are three big islands, Juana Ramírez, del Toro, and del Idolo, as well as several small isles. The streams La Laja, Cucharas, San Jerónimo, Tancochín, Tampache, and Milpas enter the lagoon along its western banks and contribute fresh water seasonally. Salinity varies from 22‰ to 38‰, water temperature from 28°C to 35°C during the dry summers and from 22°C to 27°C during the rainy winters and northers, and the maximum depth is 4 m (Fig. 1). Studies on this lagoon include those on fish (Díaz et al., 2000; Gaspar, 2007), isopods (Bortolini et al., 2012), shrimp (Cid and Raz-Guzmán, 2011), decapod crustaceans (Raz-Guzmán and Sánchez, 1996), mollusks (García-Cubas and Reguero, 1993), and pollution by heavy metals (Palomares-García et al., 2009).

Laguna Madre is the largest coastal lagoon in Mexico, with 200,000 ha and a length of 200 km. It is located at 23°45′–25°27′N and 97°23′–97°52′W. To the north lies the Río Bravo delta and to the south the Río Soto la Marina. In 1996 the sand barrier was breached by five inlets: Boca de Mezquital, Boca Ciega, Boca de Catán, Boca de Caballo, and Boca Soto la Marina. Its location in a semiarid area, its limited interaction with the sea and the reduced input of freshwater from the Río San Fernando make it a hypersaline system with salinities of 33‰ to 62‰, water temperatures of 25°C to 35°C in summer and 19°C to 25°C in winter, and a maximum depth of 4 m (Fig. 2). This lagoon has been studied unevenly, with a greater intensity in the central region and a greater emphasis on certain taxonomic groups. Studies have included peracarids (Barba and Sánchez, 2005), shrimp (Cid and Raz-Guzmán, 2011), hermit crabs (Raz-Guzmán and Sánchez, 1998), fiddler crabs (Thurman, 1987), decapods and fish (Barba, 1999), fish (Raz-Guzmán and Huidobro, 2002), birds (Contreras-Balderas, 1993), an environmental study (García-Gil et al., 1993), and a treatise on the two Laguna Madre systems, in Tamaulipas and Texas (Tunnell and Judd, 2002).

Both lagoons may be divided into a northern, central, and southern region, and Madre includes Laguna de Catán as well. Also recognized are the areas called "costa mar" (along the inner margin of the sand barriers) where the shoalgrass *Halodule wrightii* Aschers. forms meadows, and "costa tierra" (along the western margin of the lagoons) where great amounts of macroalgae are established. These last include the green algae *Halimeda incrassata* (Ellis) Lamouroux syn. *Halimeda tridens*; the brown algae *Dictyota dichotoma* (Hudson) Lamouroux and *Rosenvingea intricata* (J. Agardh) Börgensen; and the red algae *Hypnea cervicornis* J. Agardh, *Gracilaria blodgettii* Harvey, *Gracilaria cylindrica* Börgensen, *Chondria littoralis* Harvey, and *Digenea simplex* (Wulfen) C. Agardh. Mangroves of *Rhizophora mangle* L., *Avicennia germinans* (L.) L., *Laguncularia racemosa* (L.) C.F. Gaertner, and *Conocarpus erectus* L. are found in Laguna de Tamiahua, whereas in Laguna Madre *A. germinans* is present only in the extreme south.

Sampling design and data analyses.—Sampling took place in August and December 1996 in order to represent the two main climatic seasons of the region. Sampling stations were distributed throughout the lagoons. In Laguna de Tamiahua, 34 localities were sampled in August and 23 in December (Fig. 1), and in Laguna Madre 75 localities were sampled in August and 32 in December (Fig. 2). Note: locality names in Figures 1 and 2 are those where amphipods were collected.

At each locality in both lagoons, data were recorded for depth with a Secchi disk, water temperature with a field thermometer, and salinity with a refractometer (Laguna de Tamiahua, Table 1; Laguna Madre, Table 2).

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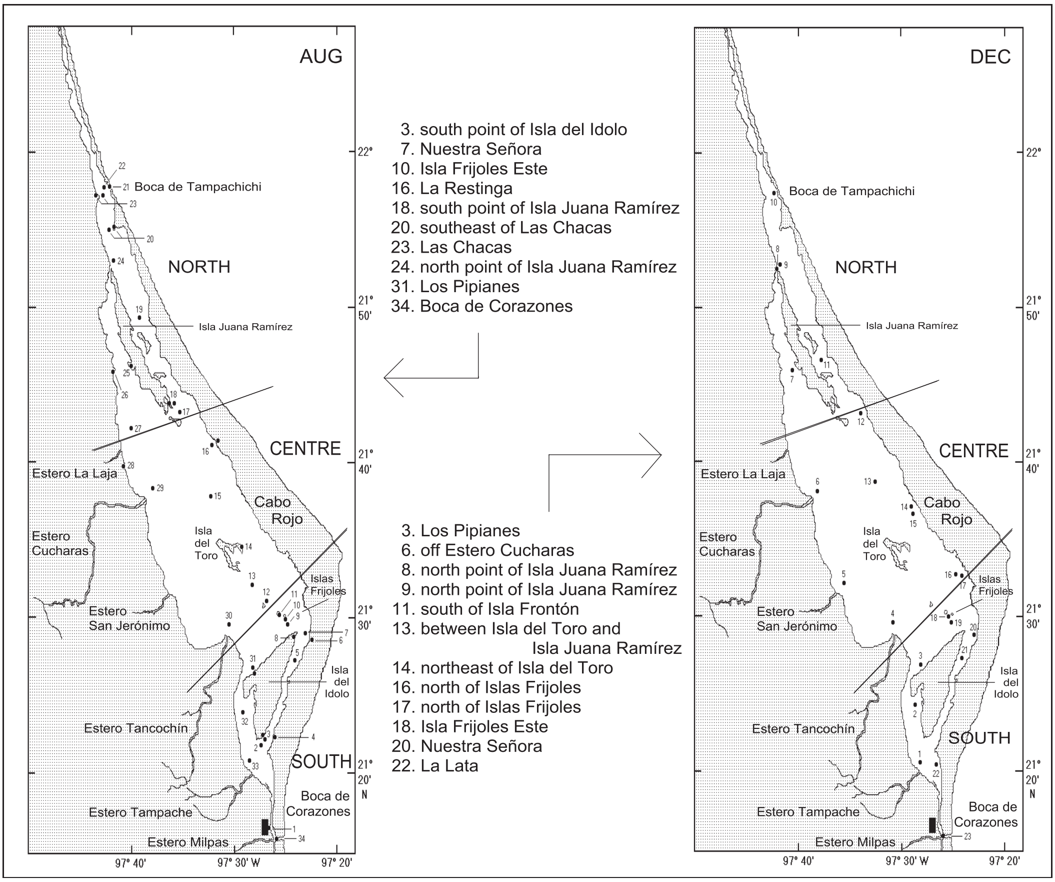

Fig. 1. Laguna de Tamiahua toponymy, regions, and sampling stations in August (left) and December (right).

Epifaunal samples were collected with two different nets in order to obtain both smaller-shallower (Renfro) and larger-deeper (otter trawl) specimens from different habitats: a Renfro beam net (1 mm mesh size, 50 m^2 sampling area) and an otter trawl (1 cm mesh size, 1.5–3 min catch per unit effort). All samples were preserved in 10% formalin. Once in the lab, the amphipods were transferred to a solution of glycerin and 70% alcohol for whitening previous to dissection. The genera and species were identified following Barnard (1969), Bousfield (1973), Myers (1982), Myers and McGrath (1984), Ledoyer (1986), Conlan (1990), Barnard and Karaman (1991), Thomas (1993a), LeCroy (2000, 2002, 2004, 2007), Myers and Lowry (2003), Appadoo and Myers (2004), and Serejo (2004). The assignment of genera to families follows Bousfield (1973), Martin and Díaz (2003), and LeCroy (2002, 2004, 2007). Exceptions are the Corophiidae that follow Myers and Lowry (2003) and the talitridan stat. nov. that follow Serejo (2004). The species list follows Martin and Davis (2001) for the Suborder Gammaridea, Myers and Lowry (2003) for the Suborder Corophiidea, with an updating following Ahyong et al. (2011) and Horton et al. (2013).

The specimens of each species were counted in order to obtain density data as individuals per square meter (ind/m^2) for the Renfro and individuals per minute (ind/min) for the otter trawl. An Olmstead–Tükey analysis was applied to the density and spatial frequency data to identify the dominant, frequent, abundant, and rare species. Maps were prepared to graphically represent the spatial and temporal distribution of the species collected with the two nets. The specimens were kept in the Laboratorio de Ecología del Bentos of the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México.

The amphipod species of the four largest lagoons along the Mexican Gulf of Mexico were

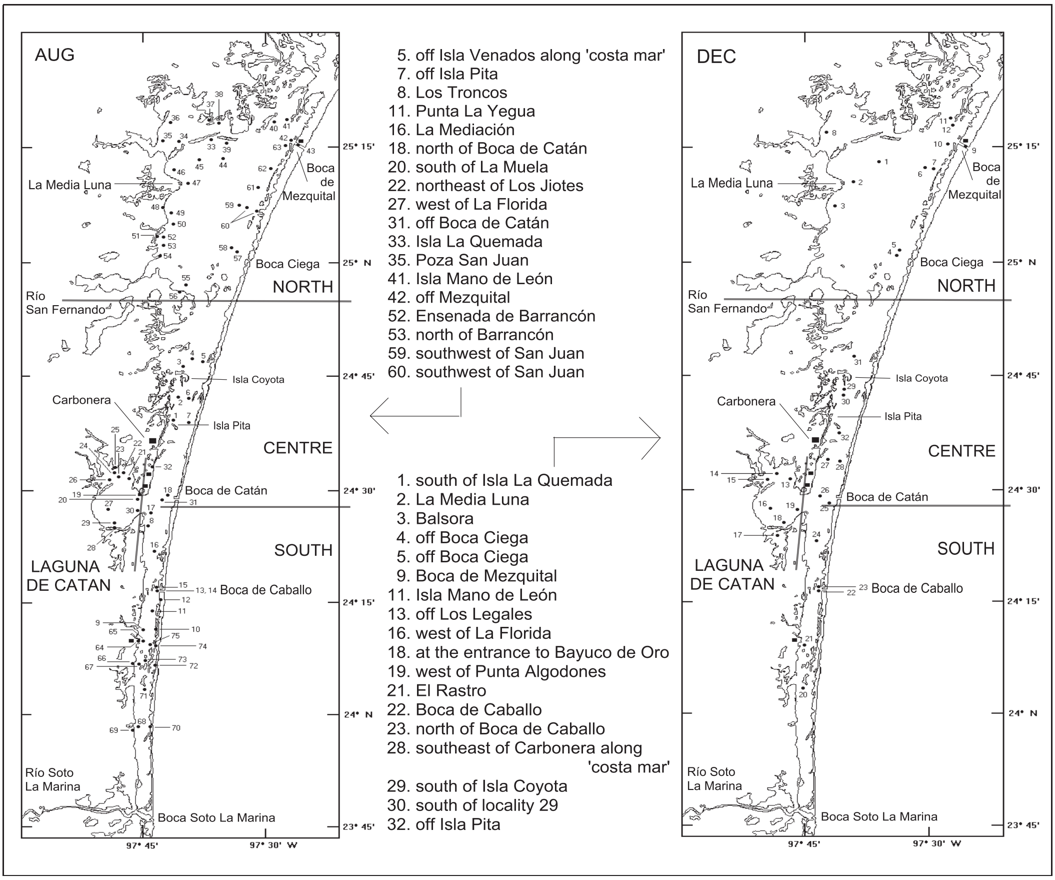

Fig. 2. Laguna Madre toponymy, regions, and sampling stations in August (left) and December (right).

compared. These are Laguna de Términos, Laguna de Alvarado, Laguna de Tamiahua, and Laguna Madre.

Results

The amphipods collected in Laguna de Tamiahua were 6,399 specimens of 12 species and nine families, to which were added five species and three families collected by Winfield and Ortiz (2011), for a total of 17 species and 12 families. Laguna Madre provided 13,251 amphipods of 18 species and 14 families, to which were added three species collected by Barba and Sánchez (2005) and another three species collected by Ortega (2013), for a total of 24 species and 14 families. The details per species for August and December are presented in Table 3. The following list of species for Laguna Madre (LM) and Laguna de Tamiahua (Lt) includes those recorded by Barba and Sánchez (2005 + for Laguna Madre), Winfield and Ortiz (2011 ++ for Laguna de Tamiahua) and Ortega (2013 +++ for Laguna Madre).

Subphylum Crustacea Brünnich, 1772
- Class Malacostraca Latreille, 1802
- Subclass Eumalacostraca Grobben, 1892
  - Superorder Peracarida Calman, 1904
  - Order Amphipoda Latreille, 1816
  - Suborder Gammaridea Latreille, 1802 (sensu Martin and Davis, 2001)
    - Ampeliscidae Krøyer, 1842
      - *Ampelisca vadorum* Mills, 1963 LM Lt
      - *Ampelisca venetiensis* Shoemaker, 1916 ++
      - *Ampelisca verrilli* Mills, 1967 ++
    - Amphilochidae Boeck, 1871
      - *Hourstonius laguna* (McKinney, 1978) LM Lt
    - Bateidae Stebbing, 1906
      - *Batea catharinensis* F. Müller, 1865 LM
    - Dexaminidae Leach, 1814

TABLE 1. Depth, water temperature, salinity, and submerged aquatic vegetation (SAV) for the Laguna de Tamiahua localities sampled in August and December 1996, where amphipods were collected.[a]

Locality and date	Loc no.	Depth (cm)	Temp (°C)	Sal (‰)	SAV	Net
August 12						
Southern point of Isla Idolo	3	40	31	33	Hal	R
Nuestra Señora	7	60	—	—	Hal	R
Isla Frijoles Este	10	90	31.5	24	—	R
La Restinga	16	30	32	27	Hal	R
August 13						
Southern point of Isla Juana Ramírez	18	20	30	30	Hal	R
Southeast of las Chacas	20	60	29.5	28	Hal	R
Las Chacas	23	80	31	26	Hal	R
Northern point of Isla Juana Ramírez	24	90	32	24	MA	OT
August 14						
Los Pipianes	31	30	29	33	Hal	R
Boca de Corazones	34	>200	28	34	MA	OT
December 13						
Los Pipianes	3	20	22.5	29	Hal, MA	R
Off Estero Cucharas	6	200	24	29	MA	OT
Northern point of Isla Juana Ramírez	8	70	25	30	—	R
Northern point of Isla Juana Ramírez	9	160	25.5	30	—	OT
South of Isla Frontón	11	200	25	30	Hal	OT
Between Isla Juana Ramírez and Isla del Toro	13	170	26	28	—	OT
Northeast of Isla del Toro	14	70	26.5	27	—	R
North of Isla Frijoles	16	190	24.5	28	Hal	OT
North of Isla Frijoles	17	190	24.5	28	Hal	R
Isla Frijoles Este	18	30	26	28	Hal	R
Nuestra Señora	20	35	27	28	Hal, MA	R
La Lata	22	40	27	30	Hal	R

[a] Hal, *Halodule wrightii*; MA, macroalgae; R, Renfro, OT, otter trawl.

Nototropis minikoi (A.O. Walker, 1905) LM Lt
Gammaridae Leach, 1814
Gammarus mucronatus Say, 1818 LM Lt
Hyalidae Bulycheva, 1957
Apohyale prevostii (H. Milne Edwards, 1830) LM Lt
Parhyale hawaiensis (Dana, 1853) +++
Melitidae Bousfield, 1983
Elasmopus levis (S.I. Smith, 1873) LM Lt
Elasmopus pectenicrus (Bate, 1862) +++
Elasmopus rapax Costa, 1853 +++
Melita nitida S.I. Smith, 1873 LM Lt
Phoxocephalidae G.O. Sars, 1891
Eobrolgus spinosus (Holmes, 1905) LM ++
Talitridae Rafinesque, 1815
Orchestia gammarellus (Pallas, 1766) +
Orchestia grillus (Bosc, 1802) LM
Suborder Corophiidea Leach, 1814 (sensu Myers and Lowry, 2003)
Infraorder Corophiida Leach, 1814
Superfamily Aoroidea Stebbing, 1899
Aoridae Stebbing, 1899
Grandidierella bonnieroides Stephensen, 1948 LM
Lembos websteri Bate, 1857 +
Unciolidae Myers et Lowry, 2003
Unciola serrata Shoemaker, 1945 ++
Superfamily Corophioidea Leach, 1814
Ampithoidae Stebbing, 1899
Ampithoe longimana S.I. Smith, 1873 LM Lt
Ampithoe valida S.I. Smith, 1873 LM Lt
Cymadusa compta (S.I. Smith, 1873) LM Lt
Corophiidae Leach, 1814
Monocorophium acherusicum (Costa, 1851) Lt
Monocorophium tuberculatum (Shoemaker, 1934) LM
Infraorder Caprellida Leach, 1814
Superfamily Microprotopoidea Myers et Lowry, 2003
Microprotopidae Myers et Lowry, 2003
Microprotopus raneyi Wigley, 1966 LM
Superfamily Photoidea Boeck, 1871
Ischyroceridae Stebbing, 1899

TABLE 2. Depth, water temperature, salinity, submerged aquatic vegetation (SAV), and sampling net for the Laguna Madre localities sampled in August and December 1996, where amphipods were collected.[a]

Locality and date	Loc no.	Depth (cm)	Temp (°C)	Sal (‰)	SAV	Net
August 2						
Off Isla Venados	5	110	31	37	Hal, MA	R, OT
Off Isla Pita	7	140	30	35	MA	OT
August 3						
Los Troncos	8	170	28	42	Hal	OT
Los Troncos	8	30	28	42	Hal	R
Punta La Yegua	11	100	30	42	MA	R
La Mediación	16	150	28	35	MA	OT
August 4						
North of Boca de Catán	18	150	30	40	MA	OT
South of La Muela	20		29	45	MA	OT
Northeast of Los Jiotes	22	120	28	51	MA	R
West of La Florida	27	140	29	50		OT
Off Boca de Catán	31	150	28	33	MA	OT
August 6						
Isla La Quemada	33	120	29	53	Hal, MA	OT
Isla La Quemada	33	30	29	53	Hal, MA	R
Poza San Juan	35	120	29	50	Hal, MA	R
Poza San Juan	35	175	29	51		OT
Isla Mano de León	41	30	35	47	MA	R
Off Mezquital	42	30	31	39	Hal, MA	R
August 7						
Ensenada de Barrancón	52	40	32	46	Hal	R
North of Barrancón	53	180	30	44	MA	OT
Southwest of San Juan	59	170	31	50	MA	OT
Southwest of San Juan	60	70	33	46	Hal, MA	R
December 6						
South of Isla La Quemada	1	350	20	40		OT
La Media Luna	2	170	19.5	40		OT
Balsora	3	235	19.5	39		OT
Off Boca Ciega	4	200	20	39		OT
Off Boca Ciega	5	70	22	37	Hal	R
Boca de Mezquital	9	100	22	38	Hal, MA	R
Isla Mano de León	11	150	22	36	Hal	OT
December 8						
Off Los Legales	13	122	21	36	Hal	OT
West of La Florida	16	250	20	39	Hal	OT
Inlet to Bayuco de Oro	18	60	21	37	Hal	R
West of Punta Algodones	19	200	20.5	37		OT
December 9						
El Rastro	21	160	20	40		OT
Boca de Caballo	22	300	22	37		OT
North of Boca de Caballo	23	80	22	37	MA	R
December 10						
Southeast of Carbonera	28	50	21	37	MA	R
South of Isla Coyota	29	30	21.5	35	Hal	R
South of locality 29	30	60	21.5	35	Hal, MA	OT
Off Isla Pita	32	40	24.5	37	Hal	R

[a] Hal, *Halodule wrightii*; MA, macroalgae; R, Renfro, OT, otter trawl.

Cerapus tubularis Say, 1817 LM
Ericthonius brasiliensis (Dana, 1853) LM Lt
Jassa falcata (Montagu, 1808) +
Photidae Boeck, 1871
Photis longicaudata (Bate et Westwood, 1862) ++

An Olmstead–Tükey analysis provided different species classifications for the samplings of

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Table 3. Amphipod abundance (No. of individuals, Renfro + otter trawl) in Laguna Madre (LM) and Laguna de Tamiahua (Lt).[a]

	Lt			LM		
Species	Aug	Dec	Total	Aug	Dec	Total
Ampelisca vadorum	1	1	2		2	2
Ampelisca venetiensis			++			
Ampelisca verrilli			++			
Hourstonius laguna	4	3	7	29	560	589
Batea catharinensis				715	79	794
Nototropis minikoi		2	2	29	90	119
Gammarus mucronatus	827	20	847	23	19	42
Apohyale prevostii	791		791		5	5
Parhyale hawaiensis						+++
Elasmopus levis	2	78	80	859	1,825	2,684
Elasmopus pectenicrus						+++
Elasmopus rapax						+++
Melita nitida	51	3	54		1	1
Eobrolgus spinosus			++	1		1
Orchestia gammarellus						+
Orchestia grillus					13	13
Grandidierella bonnieroides				43	12	55
Lembos websteri						+
Unciola serrata			++			
Ampithoe longimana		1	1	9	1	10
Ampithoe valida		76	76	3	1	4
Cymadusa compta	2,498	1,742	4,240	3,222	4,832	8,054
Monocorophium acherusicum	46	8	54			
Monocorophium tuberculatum				79	123	202
Microprotopus raneyi				1		1
Cerapus tubularis				1		1
Ericthonius brasiliensis	34	211	245	452	222	674
Jassa falcata						+
Photis longicaudata			++			
Total abundance (No. ind)	4,254	2,145	6,399	5,466	7,785	13,251
No. of species	9	11	12 + 5 = 17	14	15	18 + 6 = 24

[a] Species collected by + Barba and Sánchez (2005), ++ Winfield and Ortiz (2011), +++ Ortega (2013).

Table 4. Laguna de Tamiahua dominant (****), spatially frequent (***), and rare (*) amphipod species.[a]

	Aug		Dec	
Species	R	OT	R	OT
Ampelisca vadorum	*	—	*	—
Hourstonius laguna	*	***	—	***
Ampithoe longimana	—	—	*	—
Ampithoe valida	—	—	—	*
Cymadusa compta	****	****	****	****
Monocorophium acherusicum	***	***	***	—
Nototropis minikoi	—	—	***	—
Gammarus mucronatus	****	***	***	***
Apohyale prevostii	—	***	—	—
Ericthonius brasiliensis	***	***	****	***
Elasmopus levis	*	—	—	*
Melita nitida	*	—	***	—

[a] R, Renfro; OT, otter trawl. No species were recorded with a high density and low spatial frequency (**).

the 2 mo and two nets in the two lagoons. Generally speaking, in Laguna de Tamiahua *C. compta* was by far the dominant species, five species were spatially frequent, four species were rare, and two species varied in classification in the different samplings (Table 4).

In Laguna Madre, in general, *C. compta* was dominant, *E. levis* was mostly dominant, *M. tuberculatum* was spatially frequent, 10 species were rare, and five species were undetermined (Table 5).

Laguna de Tamiahua: Sampling with the Renfro Beam Net

Spatial distribution, August.—Amphipod distribution in August was widespread, though concentrated along "costa mar" in *Halodule wrightii* seagrass beds. The greatest species richness was recorded in the center in La Restinga (loc. 16,

TABLE 5. Laguna Madre dominant (****), spatially frequent (***), and rare (*) amphipod species.[a]

Species	Aug R	Aug OT	Dec R	Dec OT
Ampelisca vadorum	—	—	*	—
Hourstonius laguna	***	***	****	*
Ampithoe longimana	*	—	*	—
Ampithoe valida	*	—	*	—
Cymadusa compta	****	****	****	****
Grandidierella bonnieroides	***	*	***	*
Batea catharinensis	*	****	*	***
Monocorophium tuberculatum	***	***	***	***
Nototropis minikoi	*	***	*	****
Gammarus mucronatus	*	*	*	*
Apohyale prevostii	—	—	*	—
Microprotopus raneyi	*	—	—	—
Cerapus tubularis	—	*	—	—
Ericthonius brasiliensis	***	****	***	****
Elasmopus levis	***	****	****	****
Melita nitida	—	—	*	—
Eobrolgus spinosus	—	*	—	—
Orchestia grillus	—	—	*	*

[a] R, Renfro; OT, otter trawl. No species were recorded with a high density and low spatial frequency (**).

six species), while the greatest densities were recorded in the north and center for two species: *C. compta* in Las Chacas (loc. 23, 6.96 ind/m^2), the southern point of Isla Juana Ramírez (loc. 18, 13.56 ind/m^2), and La Restinga (loc. 16, 21.46 ind/m^2); and *G. mucronatus* in La Restinga (loc. 16, 6.82 ind/m^2).

Spatial distribution, December.—The amphipods collected in December had a similar distribution to that in August, with the greatest number of species in Isla Frijoles Este (loc. 18, seven species) and the greatest density in the same locality for *C. compta* (loc. 18, 5.68 ind/m^2) (Fig. 3).

LAGUNA DE TAMIAHUA: SAMPLING WITH THE OTTER TRAWL

Spatial distribution, August.—Most of the amphipods collected in August with this net were found in the northern region of the lagoon. Five species were recorded for the northern point of Isla Juana Ramírez (loc. 24) in an area rich in macroalgae, whereas only *A. prevostii* was collected in Boca de Corazones (loc. 34). *Cymadusa compta* was the only species recorded with a high density of 83.33 ind/min in locality 24.

Spatial distribution, December.—The amphipods collected in December were distributed in the north and center, in localities with *H. wrightii* and macroalgae. The greatest species richness was recorded in the northern point of Isla Juana Ramírez (loc. 9, six species), while the greatest densities were recorded for *C. compta* in the same locality with 384 ind/min and off Estero Cucharas (loc. 6) with 22.67 ind/min, for *E. levis* and *A. valida* in locality loc. 9 with 26 ind/min and 25.33 ind/min, respectively, and for *E. brasiliensis* in locality 6 with 30 ind/min (Fig. 4).

The spatial distribution of the amphipods presented some interesting patterns. Five species were widely distributed throughout the lagoon: *H. laguna*, *C. compta*, *M. acherusicum*, *G. mucrona-*

TABLE 6. Presence of amphipod species in the three regions of Laguna de Tamiahua in August and December.[a]

Species	Aug R N	Aug R C	Aug R S	Aug OT N	Aug OT C	Aug OT S	Dec R N	Dec R C	Dec R S	Dec OT N	Dec OT C	Dec OT S
Ampelisca vadorum	X								X			
Hourstonius laguna			X	X						X	X	
Ampithoe longimana								X				
Ampithoe valida										X		
Cymadusa compta	X	X	X	X			X	X	X	X	X	
Monocorophium acherusicum	X	X	X	X				X	X			
Nototropis minikoi								X	X			
Gammarus mucronatus	X	X	X	X			X		X	X	X	
Apohyale prevostii						X						
Ericthonius brasiliensis	X	X		X			X	X	X	X	X	
Elasmopus levis		X								X		
Melita nitida		X							X			
No. of species	5	6	4	5	0	1	3	5	7	6	4	0

[a] N, north; C, center; S, south; R, Renfro; OT, otter trawl.

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TABLE 7. Presence of amphipod species in the four regions of Laguna Madre in August and December.[a]

Species	Month, net, and locality															
	Aug R				Aug OT				Dec R				Dec OT			
	N	CE	CA	S	N	CE	CA	S	N	CE	CA	S	N	CE	CA	S
Ampelisca vadorum										X	X					
Hourstonius laguna	X			X	X		X	X	X	X		X	X			
Ampithoe longimana	X								X							
Ampithoe valida	X								X							
Cymadusa compta	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Grandidierella bonnieroides	X			X	X				X	X				X	X	
Batea catharinensis				X		X	X	X				X	X		X	X
Monocorophium tuberculatum	X			X		X	X	X	X	X		X	X			X
Nototropis minikoi				X	X	X	X	X	X			X	X			X
Gammarus mucronatus	X							X	X							X
Apohyale prevostii										X						
Microprotopus raneyi	X															
Cerapus tubularis					X											
Ericthonius brasiliensis	X			X	X	X	X	X	X	X		X	X		X	X
Elasmopus levis	X		X	X	X	X	X	X	X	X		X	X	X	X	X
Melita nitida												X				
Eobrolgus spinosus								X								
Orchestia grillus										X				X		
No. of species	10	1	2	8	7	6	7	9	10	9	2	8	7	4	5	7

[a] N, north; CE, center; CA, Catán; S, south; R, Renfro; OT, otter trawl.

tus, and *E. brasiliensis*. *Elasmopus levis* was present in the northern and central regions. *Ampelisca vadorum* was present in the north and south. *Nototropis minikoi* and *M. nitida* were present in the center and south. *Ampithoe valida* was recorded only in the north, *A. longimana* only in the center, and *A. prevostii* only in the south (Table 6).

Temporal distribution.—The Renfro beam net collected the same number of species (eight) in August and December, of which only two presented higher density values, *C. compta* (max. 21.46 ind/m^2) and *G. mucronatus* (max. 6.82 ind/m^2) in August, and only, *C. compta* (max. 5.68 ind/m^2), in December. Also, these maximum density values of August were noticeably greater than the maximum value of December. In the case of the otter trawl, this net collected the same number of species (six) in August and December. Only *C. compta* (max. 83.33 ind/min) presented a high density value in August, while four species presented high values in December: *C. compta* (max. 384 ind/min), *E. brasiliensis* (30 ind/min), *E. levis* (26 ind/min), and *A. valida* (25.33 ind/min). The August value was greater than the December values, except for the exceptional 384 ind/min of *C. compta* recorded in December.

Laguna Madre: Sampling with the Renfro Beam Net

Spatial distribution, August.—The amphipods collected in August were distributed mainly throughout the northern region of the lagoon, with the greater number of species off Mezquital (loc. 42, nine species), Los Troncos (loc. 8, five species), and Punta La Yegua (loc. 11, five species). The greatest density was recorded for *C. compta* in locality 8 with 60.56 ind/m^2.

Spatial distribution, December.—The amphipods collected in December presented a more even distribution, with the greater number of species in La Media Luna (loc. 2, nine species) and north of Boca de Caballo (loc. 23, eight species), followed by a locality southeast of Carbonera (loc. 28, six species), off Isla Pita (loc. 32, five species), south of Isla Coyota (loc. 29, five species), and Boca de Mezquital (loc. 9, five species). The greatest densities were recorded for *C. compta* in loc. 28 with 62.64 ind/m^2 and loc. 23 with 96.2 ind/m^2 (Fig. 5).

Laguna Madre: Sampling with the Otter Trawl

Spatial distribution, August.—The amphipods collected in August with this net were distributed throughout the lagoon, though with a greater

TABLE 8. Presence of amphipod species in Laguna de Términos (LT), Laguna de Alvarado (LA), Laguna de Tamiahua (Lt), and Laguna Madre (LM).[a]

Species	LT	LA	Lt	LM
Ampelisca vadorum	1, 3		10	10
Ampelisca venetiensis ++			8	
Ampelisca verrilli ++			8	
Hourstonius laguna	1, 3, 5	5, 7, 8	10	10
Batea catharinensis				6, 9, 10
Nototropis minikoi	1, 5	5, 8	10	6, 10
Gammarus mucronatus	1, 5	2, 5, 7, 8	8, 10	6, 9, 10
Apohyale prevostii			10	6, 10
Parhyale hawaiensis +++				9
Elasmopus levis	1, 3	8	10	6, 9, 10
Elasmopus pectenicrus +++				9
Elasmopus rapax +++				9
Melita nitida	3		10	10
Eobrolgus spinosus	1, 3		8	10
Orchestia gammarellus +				6, 9
Orchestia grillus				10
Grandidierella bonnieroides	1, 3, 5	2, 4, 5, 7, 8		9, 10
Lembos websteri +				6
Unciola serrata ++			8	
Ampithoe longimana			10	10
Ampithoe valida			10	10
Cymadusa compta	1, 3, 5	5	10	6, 9, 10
Monocorophium acherusicum			10	
Monocorophium tuberculatum				9, 10
Microprotopus raneyi				6, 10
Cerapus tubularis				6, 10
Ericthonius brasiliensis	5	5, 8	10	6, 9, 10
Jassa falcata +				6
Photis longicaudata ++			8	
Sum of species	10	8	18	24

[a] Symbols: +, Barba and Sánchez (2005); ++, Winfield and Ortiz (2011); +++, Ortega (2013). References: 1, Ledoyer (1986); 2, Winfield et al. (1997); 3, Corona et al. (2000); 4, Winfield et al. (2001); 5, Cházaro et al. (2002); 6, Barba and Sánchez (2005); 7, Winfield et al. (2007); 8, Winfield and Ortiz (2011); 9, Ortega (2013); 10, this study.

concentration near Boca de Catán. The greater numbers of species were recorded in Los Troncos (loc. 8, nine species), La Mediación (loc. 16, eight species), south of La Muela (loc. 20, seven species), off Isla Pita (loc. 7, six species), north of Barrancón (loc. 53, six species), and off Boca de Catán (loc. 31, five species). The greatest densities were recorded for *B. catharinensis* (loc. 8, 80.33 ind/min), *C. compta* (loc. 7, 89 ind/min; loc. 16, 93.33 ind/min; loc. 8, 103.67 ind/min), and *E. levis* (loc. 8, 105 ind/min).

Spatial distribution, December.—As with the Renfro beam net, the amphipods collected in December with the otter trawl presented an even distribution with the greater number of species in Boca de Caballo (loc. 22, six species), El Rastro (loc. 21, five species), and La Media Luna (loc. 2, five species). In this case, no species recorded a density greater than 80 ind/min (Fig. 6).

As in Laguna de Tamiahua, the spatial distribution of the amphipods in Laguna Madre also presented some interesting patterns. Eight species were present throughout the four regions of the lagoon: *H. laguna*, *C. compta*, *G. bonnieroides*, *B. catharinensis*, *M. tuberculatum*, *N. minikoi*, *E. brasiliensis*, and *E. levis*. *Gammarus mucronatus* was present in the northern and southern regions, and *A. vadorum* in the center and Catán. Four species were recorded only in the north, *A. longimana*, *A. valida*, *M. raneyi*, and *C. tubularis*; *A. prevostii* and *O. grillus* only in the center; and *M. nitida* and *E. spinosus* only in the south (Table 7).

Temporal distribution.—The Renfro beam net collected slightly more species in December (15) than in August (12). Of them all, *C. compta* recorded the greatest density values in both months, but with the maximum value of 96.2 ind/m^2 in December. The otter trawl, in turn, collected a similar number of species in August (11) and December (10). However, only August recorded three species with high density values, as is indicated above.

DISCUSSION

Regarding the year of sampling, it is important to make three points after having consulted the only three, more recent, studies available: (1) that only three species of 13 collected by Barba and Sánchez (2005) and three species of 12 collected by Ortega (2013) in Laguna Madre, as well as five species of six collected by Winfield

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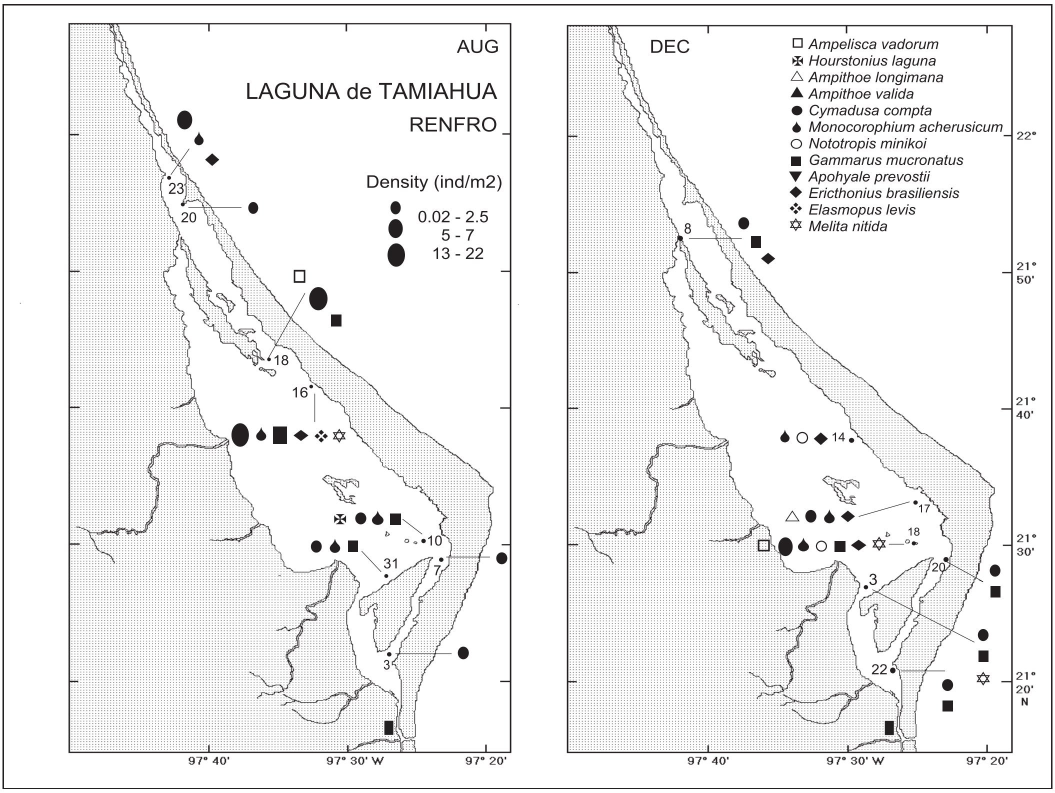

Fig. 3. Laguna de Tamiahua sampling with a Renfro beam net (August, left; December, right).

and Ortiz (2011) in Laguna de Tamiahua, were not collected in our study, (2) that our study recorded nine more species than Barba and Sánchez (2005), 11 more species than Ortega (2013), and 11 more species than Winfield and Ortiz (2011), and (3) that all the species recorded in these three papers plus ours are cited here, in view of which we consider our species list to be taxonomically updated and valid.

Of the 12 amphipod species recorded in this study for Laguna de Tamiahua, only one species was also reported by Winfield and Ortiz (2011), *G. mucronatus*, a common inhabitant of seagrass, salt marsh, macroalgae, muddy substrates, and sandy substrates (Boström and Bonsdorff, 2000; Jackson et al., 2002). The greater number of species recorded in the present study reflects the more intensive and widespread sampling this study carried out in the lagoon, as well as the more varied sampling gear used.

Of the 18 amphipod species recorded in this study for Laguna Madre, nine species were also reported by Barba and Sánchez (2005) and seven were also reported by Ortega (2013). The five species recorded by the three studies, *B. catharinensis*, *G. mucronatus*, *E. levis*, *C. compta*, and *E. brasiliensis*, are common inhabitants of seagrass beds and sandy substrates and were present in the system throughout the year. It is well known that these habitats harbor a high infaunal and epifaunal biodiversity (Boström and Bonsdorff, 2000; Jackson et al., 2002), and the variety of habitats in Laguna Madre increases the availability of a great number of microhabitats for soft-bottom and hard substrate benthic dwellers (Tunnell and Judd, 2002). The greater number of species of this study responds to the same reasons stated above for Laguna de Tamiahua, while the density values recorded here are similar to those reported by Barba and Sánchez (2005). Of interest is that while more species and the higher densities were recorded in the northern and southern regions of the lagoon, the lowest values of all were those of Laguna de Catán. This may be due to the presence of predators, since this is an area rich in fisheries species, and amphipods of the families Ampithoidae, Gammaridae, and Melitidae, which are common food items of decapods and fish,

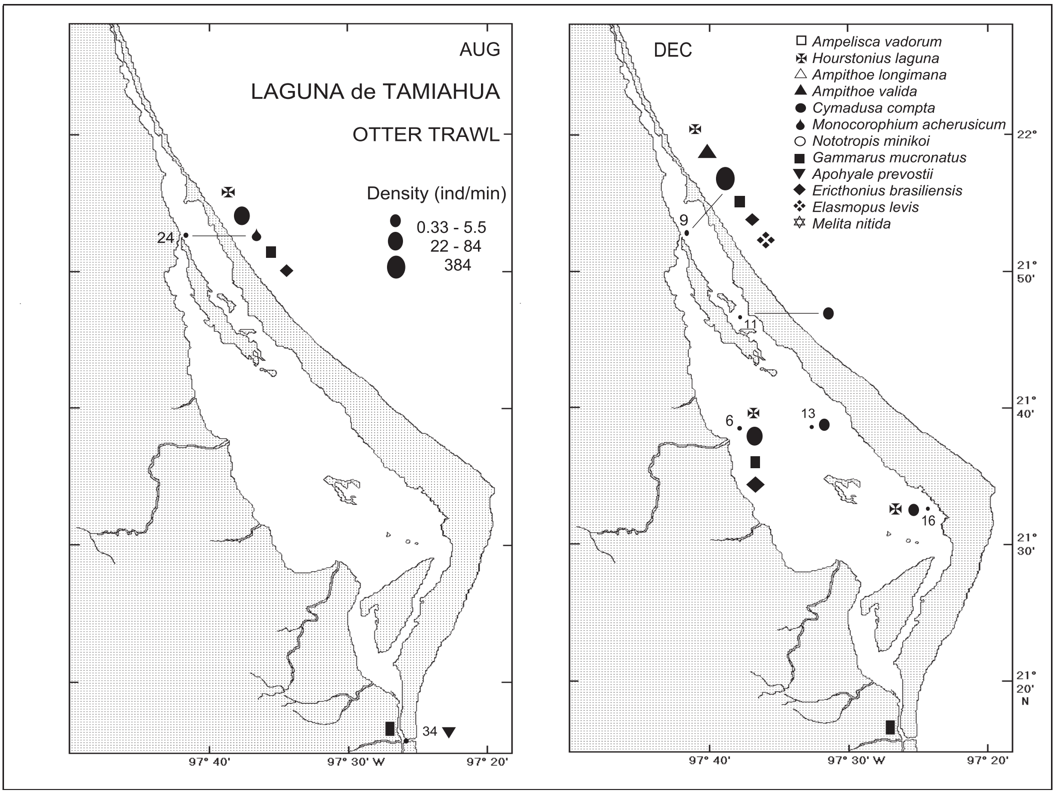

Fig. 4. Laguna de Tamiahua sampling with an otter trawl (August, left; December, right).

presented low values, while smaller amphipod species were more abundant.

Spatial distribution.—The patterns of spatial distribution of the 12 amphipod species of Laguna de Tamiahua and the 18 species of Laguna Madre are related, not so much with the regions in the lagoons, but with the seagrass and macroalgae habitats present in both systems. This agrees with many previous studies, among which some are stated below, that have recorded amphipods on submerged aquatic vegetation, as well as on detritus; oysters; muddy, sandy, and rocky substrates; and intertidal brackish waters, all of which are habitats commonly found in these two lagoons. The previously reported habitats of these species are the following.

Ampelisca vadorum, M. raneyi, and *C. tubularis* are tube dwelling species that live on seagrass and macroalgae, the first also on sand and shell in poly-euhaline shallow waters (LeCroy, 2002), the second also on sponges and oyster reefs, and the second and third also on mud and sand in shallow waters (Barba and Sánchez, 2005; LeCroy, 2007).

Hourstonius laguna, *B. catharinensis*, *N. minikoi*, *G. mucronatus*, *A. prevostii*, *E. levis*, *E. spinosus*, *A. longimana*, *A. valida*, and *C. compta* live on seagrass and macroalgae in shallow brackish and marine waters (Winfield et al., 1997; Barba and Sánchez, 2005), with *B. catharinensis* and *G. mucronatus* also on oyster reefs, mud, and sand (Winfield et al., 1997; LeCroy, 2000, 2004; Barba and Sánchez, 2005); *N. minikoi* and *E. spinosus* also on sand (Fox and Bynum, 1975; Barba and Sánchez, 2005); *A. prevostii* and *A. valida* also on intertidal rocky substrates (LeCroy, 2002, 2007; Barba and Sánchez, 2005); *E. levis* also on detritus, sand, and rock (LeCroy, 2000); *A. longimana* also on mud (LeCroy, 2002); and *C. compta* also on rocks (LeCroy, 2002; Barba and Sánchez, 2005).

Melita nitida is a fouling species that lives on seagrass, hydroids, oyster reefs, mud, and sand (LeCroy, 2000).

Orchestia grillus is a nest building species found on seagrass, macroalgae, detritus, gravel, oyster reefs, and intertidal sandy substrates (Fox and Bynum, 1975).

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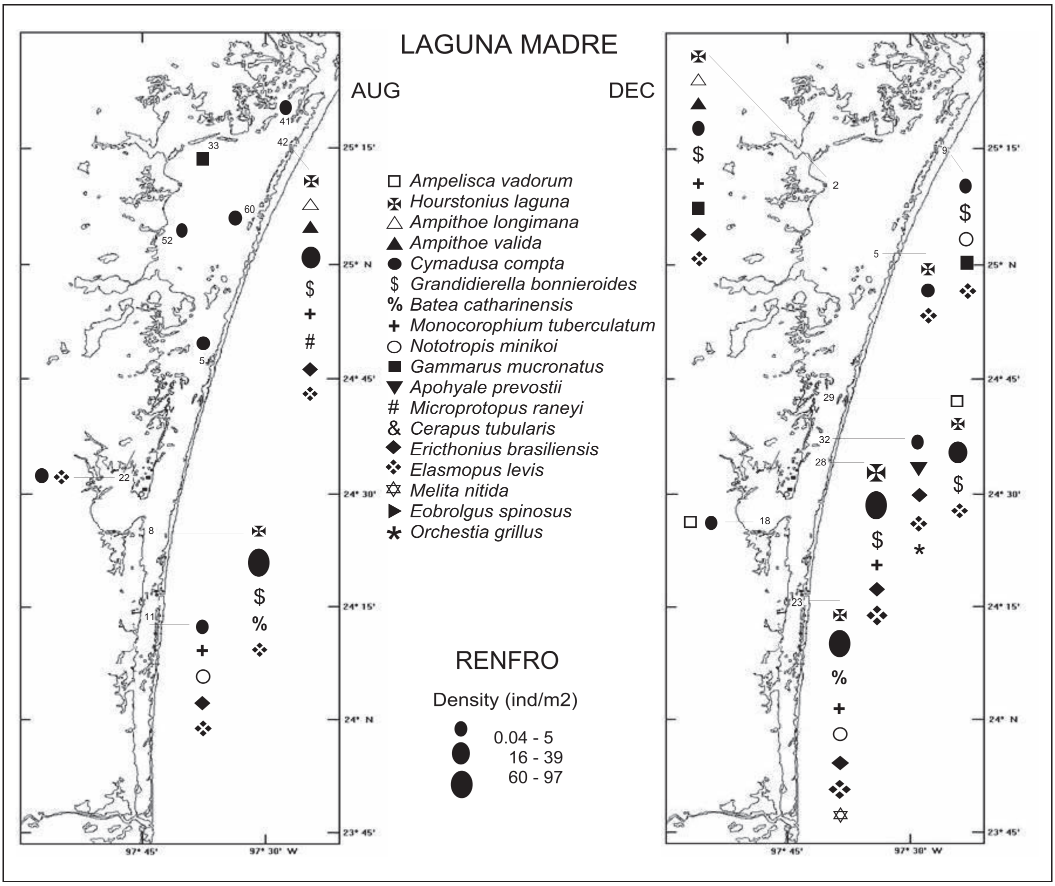

Fig. 5. Laguna Madre sampling with a Renfro beam net (August, left; December, right).

Grandidierella bonnieroides lives on seagrass (Stoner, 1983; Winfield et al., 1997), macroalgae, sponges, oyster reefs, and sand, in rivers, lagoons, salt marshes, mangroves, bays, and intertidal brackish waters (LeCroy, 2002; Martin and Díaz, 2003; Appadoo and Myers, 2004).

Monocorophium acherusicum and *E. brasiliensis* are fouling tube dwelling species that live on seagrass (Fox and Bynum, 1975), macroalgae, sponges, tunicates, hydroids, mussels, mud, and rubble, in estuaries, bays, and intertidal brackish waters (Myers, 1982; Appadoo and Myers, 2004; LeCroy, 2004, 2007; Barba and Sánchez, 2005).

Monocorophium tuberculatum lives on mud and sand in estuaries, bays, and intertidal brackish waters (LeCroy, 2004).

In general, high densities of amphipods have been recorded in both seagrass and macroalgae habitats where they find food and refuge and play an important part in trophic chains as prey (Corona et al., 2000). Previous data have shown that amphipod mortality by predation is closely related to habitat complexity, with lower mortalities in more complex habitats (Corona et al., 2000). Thus, the ecological relationship between species and habitat has been proved in various studies (Raz-Guzmán and de la Lanza, 1993), and the part that submerged aquatic vegetation plays in the recruitment of a great number of invertebrate and fish species in coastal lagoons has long been recognized (Heck and Crowder, 1991; Barba, 1999). Such is the case of the present study, where the species distribution–submerged aquatic vegetation relationship may be clearly seen.

In addition, and regarding vegetation, Raz-Guzmán and Barba (2000) observed that the distribution of seagrasses in the largest coastal lagoons of the Mexican Gulf of Mexico is regulated by salinity, turbidity, and type of substrate, indicating that variations in amphipod populations in coastal lagoons may be associated with changes in the environment. For amphipods, this suggests it may be important to

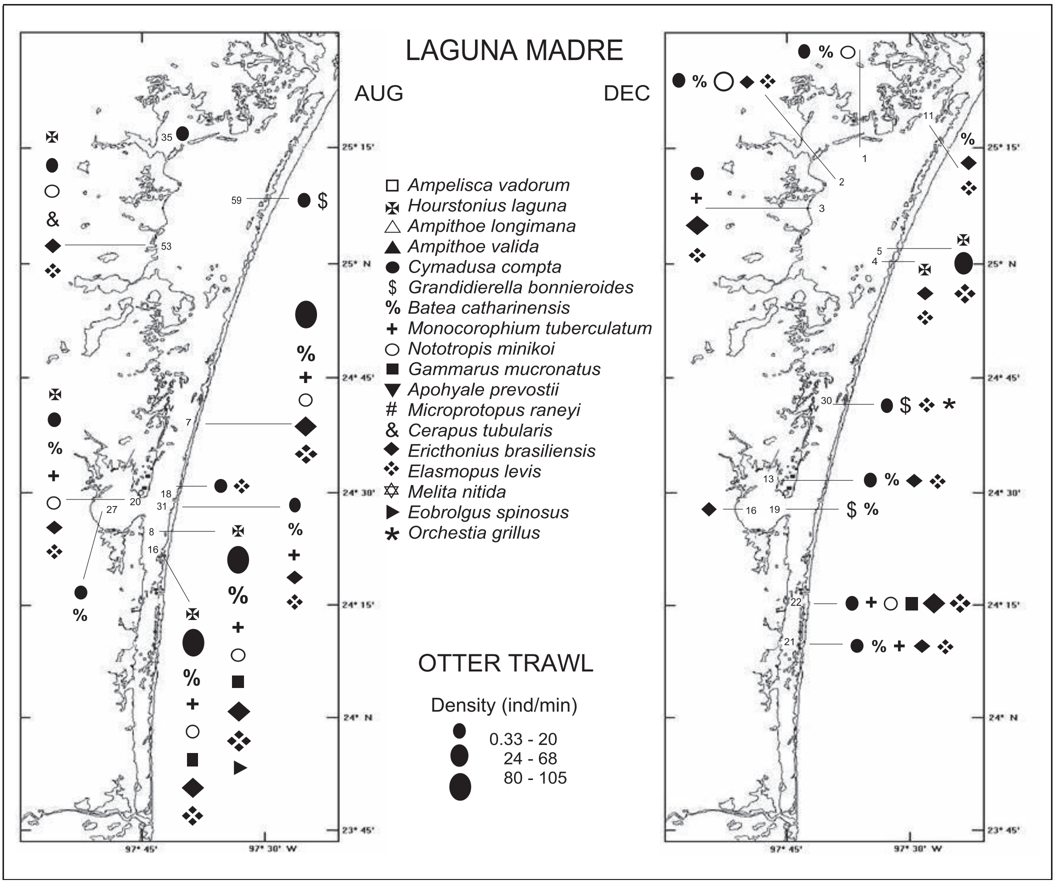

Fig. 6. Laguna Madre sampling with an otter trawl (August, left; December, right).

implement a management plan for the conservation of their habitats, taking into account their ecological relevance as the second link in trophic chains and as a potential resource for the aquaculture of economically valuable fish.

Another point of interest is that brown *Farfantepenaeus aztecus* (Ives, 1891), pink *Farfantepenaeus duorarum* (Burkenroad, 1939), and white *Litopenaeus setiferus* (Linnaeus, 1767) shrimp use both Laguna de Tamiahua and Laguna Madre as postlarvae, juveniles, subadults, and even adults throughout the year. In both lagoons, the greatest fishing effort occurs along "costa mar," coinciding with the areas of greatest shrimp density (Cid and Raz-Guzmán, 2011) and *H. wrightii* seagrass beds, and the distribution of amphipods recorded in this study agrees with the data reported for penaeid shrimp.

Temporal distribution.—Both Laguna de Tamiahua and Laguna Madre are characterized by two clearly defined seasons throughout the year influencing the hydrological behavior of the systems: a dry season from March to August and a rainy season from September to February. Temperature and salinity increase in spring and summer due to the strong heat and sunlight typical of the time of year and to the lack of freshwater runoff, and temperature and salinity decrease in autumn and winter with the arrival of the rains and the meteorological phenomenon called northers. The numbers of species recorded in August and December did not vary in Laguna de Tamiahua and varied very little in Laguna Madre. Regarding amphipod density in the two lagoons, the greater values generally recorded in August suggest that conditions are optimum for reproduction and survival, with temperatures of 28°C to 35°C and salinities of 24‰ to 53‰ providing ideal nursery, feeding, and protection habitats for the amphipods (Heck and Crowder, 1991). In contrast, the lower density values of December, coinciding with temperatures of 19°C to 27°C and salinities of 27‰ to 40‰, may reflect two circumstances: (1) that during this

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season the lagoons receive rain and wind that generate currents that may affect amphipod habitats, resuspending sediment and moving seagrasses, and/or (2) that as the lagoons provide refuge and feeding areas for migratory birds, fish, and other crustaceans, mainly those that spend the winter in tropical regions (Raz-Guzmán and Sánchez, 2001), amphipod density decreases through predation. It is well known that peracarid crustaceans form part of trophic chains as prey of coastal birds, fish, and crustaceans, an example of which are the juveniles of fish species that feed almost exclusively on small estuarine organisms during the first stages of their life cycle (Thiel and Hinojosa, 2009).

Comparison of lagoons.—The amphipod species of the four largest lagoons of the Mexican Gulf of Mexico were compared. Of the 17 species recorded here for Laguna de Tamiahua and the 24 species recorded for Laguna Madre, nine and ten, respectively, have been reported for Laguna de Términos, and six and seven, respectively, have been reported for Laguna de Alvarado. The greater similarity was that between Laguna de Tamiahua and Laguna Madre, with 12 common species (41.4%) of the 29 recorded (sampled + reported). This is ecologically relevant since Cabo Rojo, in Laguna de Tamiahua, presents a critical boundary for the northern dispersal of tropical shallow-water fauna (Thurman, 1987). However, the similarity responds to the fact that these two lagoons are environmentally very similar, with *H. wrightii* seagrass beds along "costa mar" and macroalgae along "costa tierra." The next lagoon in similarity is Laguna de Términos, where seagrass species include *Thalassia testudinum* Banks ex König, *Syringodium filiforme* Kütz, and *H. wrightii.* The least similar is Laguna de Alvarado owing to its oligo-mesohaline waters and having only *Ruppia maritima* (L.) as a seagrass species (Table 8).

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